New data on the anatomy and relationships of the Paleocene crocodylian *Akanthosuchus langstoni*

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The phylogenetic relationships of the Paleocene crocodylian *Akanthosuchus langstoni* are assessed using published data matrices and morphological data from the holotype and referred specimens. Cladistic analyses indicate that *Akanthosuchus* is unequivocally nested within Alligatoroidea. Weak support from a majority rule consensus tree indicates that *Akanthosuchus* may be more closely allied with alligatorines than with caimanines, but in the strict consensus tree these relationships remain ambiguous. There is no evidence from phylogenetic analyses to support the hypothesis that *Akanthosuchus* represents the postcrania of the Paleocene crocodylians *Navajosuchus* or *Ceratosuchus*. Growth marks observed in histological sections of osteoderms of the holotype of *Akanthosuchus langstoni* indicate that it was at least eight years old at the time of death. Although the individual may not have been fully mature at the time of death, lineage dwarfism cannot be ruled out as a possible reason for its relatively small size.

Key words: Crocodylia, Alligatoroidea, *Akanthosuchus*, osteoderms, dwarfism.

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Introduction

Akanthosuchus langstoni O'Neill, Lucas, and Kues, 1981 is a small crocodylian known from a few incomplete specimens of Paleocene (Puercan and Torrejonian) age collected in the San Juan Basin, New Mexico (O'Neill et al. 1981; Lucas 1992). Its unusual spiked and keeled osteoderms identify *Akanthosuchus* as one of the most peculiar of known Paleocene crocodylians. The type specimen (NMMNH P-8628) comprises a complete hind limb, 28 vertebrae, a single jaw fragment, and over 200 osteoderms. Referred specimens (NMMNH P-8611, P-15209, P-21565, and P-35169) constitute only a few fragments of bone and isolated osteoderms. The paucity of available material pertaining to *A. langstoni* hinders interpretations of lifestyle and phylogenetic affinities, because such interpretations for fossil crocodylians have been traditionally based on morphology of the skull instead of the evolutionarily conservative postcranial skeleton (e.g., Langston 1973). Moreover, the majority of *A. langstoni* material consists of osteoderms, exoskeletal elements that have been historically underrepresented in studies of vertebrate morphology. Recent studies (Hill 2003, 2004, 2005), however, have shown that morphological and histological data from the integument and its dermally ossified components (osteoderms) can affect phylogenetic hypotheses substantially, particularly by increasing resolution in otherwise poorly understood higher taxa. Integumentary data are especially important in taxa for which the majority of the fossil record consists of osteoderms, such as aetosaurs (Heckert and Lucas 1999) and *Akanthosuchus* (O'Neill et al. 1981).

O'Neill et al. (1981) recognized four categories of osteoderms in *Akanthosuchus* based on gross morphology: square, oval, spiked, and bladed. Because the osteoderms were found entirely disarticulated, their positions in life can only be conjectured. It is likely, however, that each type occupied a specific location on the body, and that, for example, spiked and flat osteoderms were not randomly interspersed with one another. This hypothesis is reinforced by the unequal number of osteoderms of each morphotype (O'Neill et al. 1981). Spiked osteoderms are the most numerous morphotype, comprising nearly 60% of the total osteoderm sample, followed by oval (27%), square (13%), and bladed (<1%). Intraorganismal variation in osteoderm morphology is also known in other archosaurs such as aetosaurs (Heckert and Lucas 1999, 2003) and in extant crocodylians (Ross and Meyer 1983; and see below).

In their original description of *Akanthosuchus*, O'Neill et al. (1981) tentatively suggested alligatorine affinities for the genus, based on the morphology of the partial retroarticular process. In the absence of diagnostic cranial material, these authors acknowledged that the specimen may represent the postcranium of the previously named Paleocene crocodylians *Navajosuchus* or *Ceratosuchus*. Here, we use cladistic methods to test these hypotheses, and present new information on the anatomy and histology of crocodylian osteoderms.

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Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; LACM, Los Angeles County Museum of Natural History, Los Angeles, USA; MCZ, Museum of Comparative Zoology, Cambridge, Massachusetts, USA; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA; SBU, Anatomical Sciences Museum, Stony Brook University, Stony Brook, New York, USA; UCMP, University of California Museum of Paleontology, Berkeley, California, USA.

Materials and methods

We compared the gross morphology of the osteoderms of *Akanthosuchus langstoni* with that of other fossil and extant crocodylians. Specimens examined included *Akanthosuchus langstoni* (NMMNH P-8628), *Alligator mississippiensis* (UCMP 119044; SBU Rp8), *Alligator olseni* (MCZ, uncatalogued specimen), *Allognathosuchus mooki* (AMNH 6780); "*Crocodylus*" (?=*Diplocynodon*) *butikonensis* (MCZ 3762), *C. rhombifer* (AMNH 19215; 77595), "*C.*" *robustus* (AMNH 3107), Crocodylia indet. (MCZ 17720, 17727), *Diplocynodon ratelii* (AMNH 19161 through 19166), cf. *Leidyosuchus* (LACM 45808), and *Pristichampsus vorax* (AMNH 29993).

The dorsal integument of one American alligator (*Alligator mississippiensis*; SBU Rp8) was dissected, and osteoderms representing nuchal, mid-dorsal, dorsolateral, and caudal regions were cleaned of soft tissues using bleach and a soft brush.

Three osteoderms from the type specimen of *Akanthosuchus langstoni* (one oval and two spiked) were prepared using paleohistological techniques. After being molded in silicone and cast in polyester, each specimen was sectioned at the level of its greatest dorsoventral thickness, perpendicular to the superficial expansion (keel or spike). Sections were ground to a thickness of 30 μm, polished, and permanently mounted on glass slides with cover slips. Slides were observed and digitally photographed under ordinary and cross-polarized light. Histological terminology used herein follows Curry (1999).

To test the phylogenetic affinities of *Akanthosuchus langstoni*, we scored the character data available from the type specimen for the characters used by Brochu (1999; a slightly modified version of the matrix used by Brochu [1997a]). The available material pertaining to *A. langstoni* allowed us to score six of Brochu's (1999) characters with certainty: characters 18, 35, 36, 40, 50, and 51. We also examined these characters in the context of a more recent analysis of alligatoroid phylogeny (Brochu 2004). The matrices were analyzed using an unconstrained heuristic search in NONA 2.0 (Goloboff 1994; hereafter NONA) with the following settings in effect: hold = 100,000; mult * N = 100; search strategy = Multiple TBR + TBR. As in Brochu's (1999) analysis, *Bernissartia fagesii* and the Glen Rose form were considered as outgroups, and all characters were unordered and unweighted. Results were checked against those obtained using heuristic searches in PAUP*4.0b10 (Swofford 2003).

Results

Morphology.—Re-examination of the holotype specimen of *Akanthosuchus* corroborates the earlier assessment made by O'Neill et al. (1981) of four distinct osteoderm morphotypes. We observed square, oval, spiked, and bladed osteoderms in the same proportions as reported by these authors.

Most osteoderms of *Akanthosuchus* bear a prominent expansion on the superficial surface in the form of a keel or spiked boss. Spiked osteoderms (Fig. 1A) possess blunt, conical spikes that average 0.72 times the maximum dimension of the osteoderm base (O'Neill et al. 1981). In some spiked osteoderms, the dorsoventral height actually exceeds the craniocaudal length. Bladed osteoderms (Fig. 1B) have an irregular oval base and a tall keel that is curved mediolaterally. Most oval osteoderms (Fig. 1C) possess a longitudinal keel with a roughened edge that extends along the posterior two-thirds of the superficial surface. The majority of square osteoderms are flat and lack a keel (Fig. 1D); however, some bear a very low, rounded keel. Regardless of overall morphology, the superficial surfaces of *Akanthosuchus* osteoderms are ornamented with small, shallow, ovoid pits.

The deep surfaces of *Akanthosuchus* osteoderms exhibit a finely woven texture composed of small, yet macroscopic, ossified fiber bundles (Fig. 1A_2, B_2, C_2). These fibers correspond to the "structural fibers" (similar to Sharpey's fibers) observed on the deep surfaces of some ankylosaurian osteoderms (Scheyer and Sander, 2004). The osteoderms are flat or weakly concave along their deep surfaces, and are perforated by tiny pinhole foramina, each less than one-twentieth the length of the osteoderm.

Preservation, size, and close association at the collecting locality indicate that the four osteoderm morphotypes of *Akanthosuchus langstoni*, although dissimilar, belong to one individual of one taxon (O'Neill et al. 1981). Indeed, the range of morphological variation in the osteoderms of *A. langstoni* is mirrored to a large extent by osteoderm morphology we observed in an extant alligator.

Through careful dissection of the dorsal integument, intraorganismal variation in osteoderm morphology was documented in SBU Rp8, a fresh specimen of the extant alligatorine *Alligator mississippiensis* (Fig. 2). We observed four morphologically distinct types of osteoderms, each corresponding with a particular anatomical region of the integument. Osteoderms from the nuchal region (Fig. 2A) have a thick base and a high keel that is nearly one-third the transverse dimension of the osteoderm. The superficial surfaces of these osteoderms are heavily ornamented with deep, subcircular pits.

Mid-dorsal trunk osteoderms of SBU Rp8 (Fig. 2B) are either square or slightly longer craniocaudally than they are

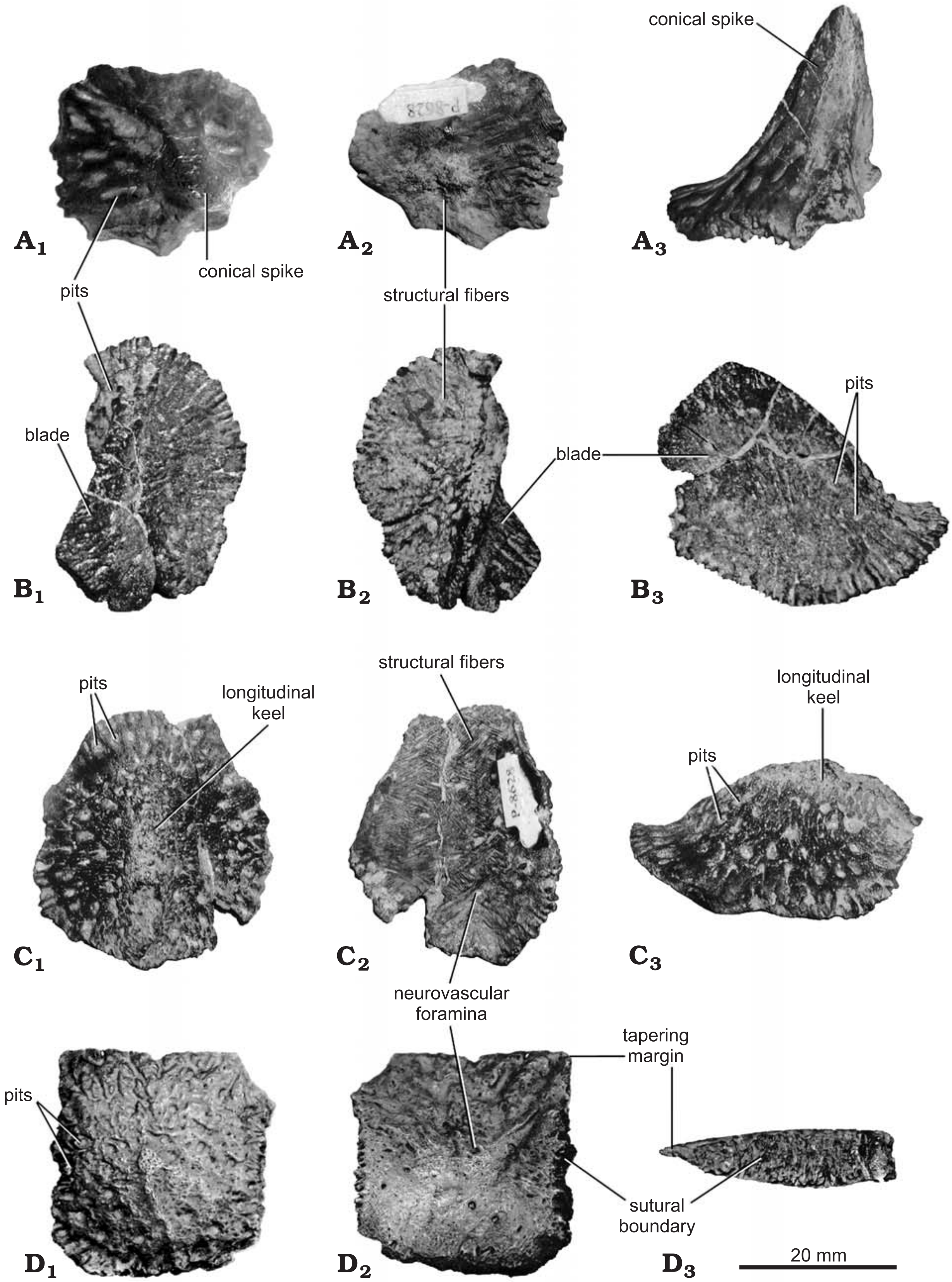

Fig. 1. *Akanthosuchus langstoni* O'Neill, Lucas, and Kues, 1981. Holotype, NMMNH P-8628, from the Middle Paleocene (Torrejonian) Nacimiento Formation, San Juan Basin, New Mexico, USA. **A**. Spiked osteoderm in superficial (A_1), deep (A_2), and lateral (A_3) views. **B**. Bladed osteoderm in superficial (B_1), deep (B_2), and lateral (B_3) views. **C**. Oval, keeled osteoderm in superficial (C_1), deep (C_2), and lateral (C_3) views. **D**. Square osteoderm in superficial (D_1), deep (D_2), and lateral (D_3) views.

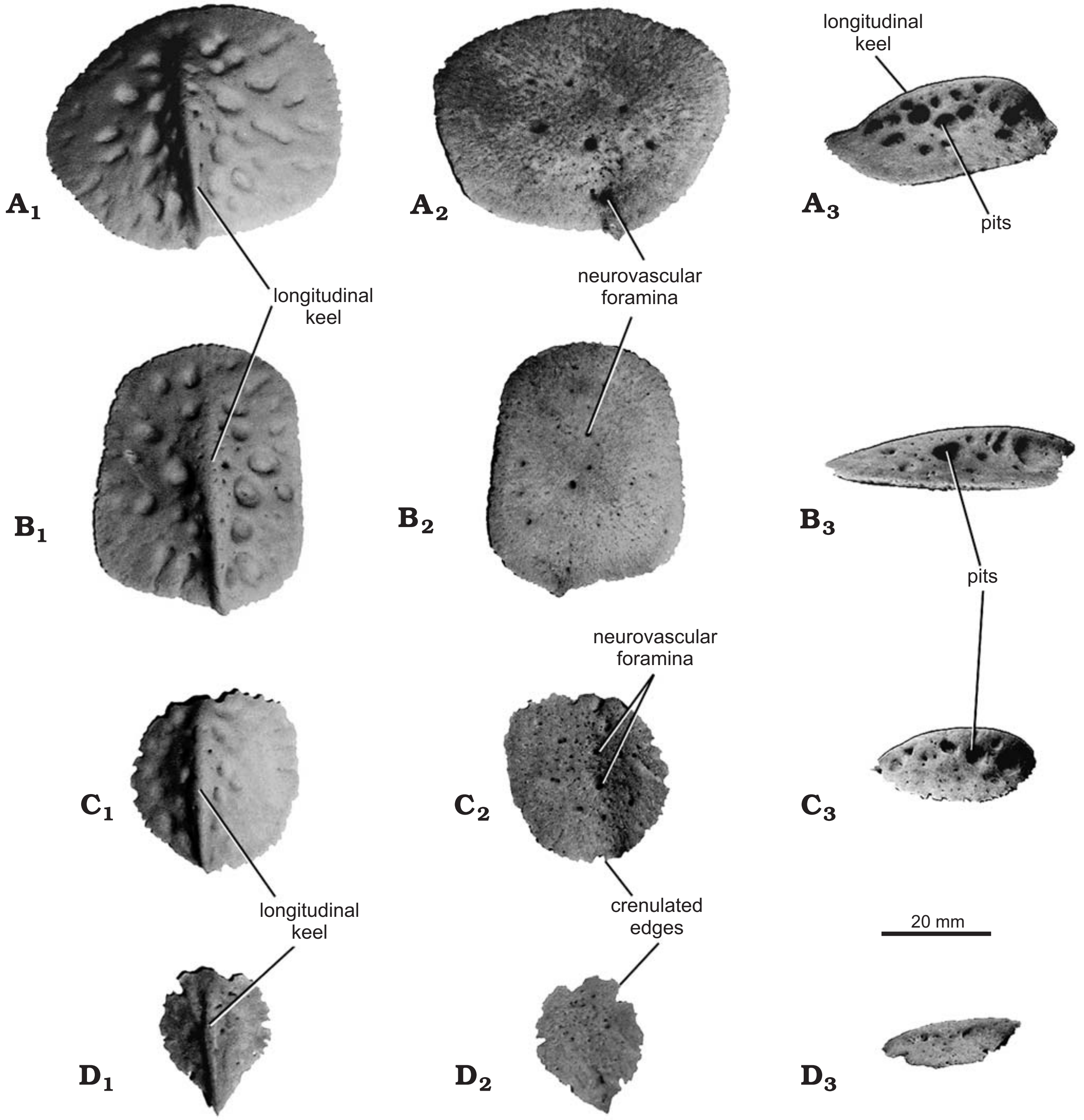

Fig. 2. *Alligator mississippiensis* Daudin, 1802. SBU Rp8, Recent, from southern Louisiana, USA. Dorsal osteoderms from different locations along the trunk. **A**. Nuchal osteoderm in superficial (A_1), deep (A_2), and lateral (A_3) views. **B**. Mid-dorsal osteoderm in superficial (B1), deep (B2), and lateral (B3) views. **C**. Dorsolateral osteoderm in superficial (C_1), deep (C_2), and lateral (C_3) views. **D**. Caudal osteoderm in superficial (D1), deep (D2), and lateral (D_3) views.

wide. They appear flat and plate-like by comparison to the thickened nuchal osteoderms. The keel is typically low and less than one-fourth the transverse dimension of the osteoderm. Pitting on the superficial surface is uniform, with a row of deep, subcircular pits on either side of the keel and radiating arrays of subcircular pits peripherally.

Osteoderms from the dorsolateral region of the integument (Fig. 2C) are ovoid, with the anteroposterior length exceeding the transverse width slightly. These osteoderms are smaller than the nuchal and mid-dorsal osteoderms, and are ornamented only by a single row of deep subcircular pits on either side of the keel. Occasionally there exist one or a few pits peripherally on the superficial surface. The keel is weakly developed in these osteoderms, as well, being only about one-fifth as high as the osteoderm is wide. The entire circumferential edges of the oval osteoderms are sharply crenulated.

Distal caudal osteoderms of SBU Rp8 (Fig. 2D) are craniocaudally longer than they are wide (sometimes three

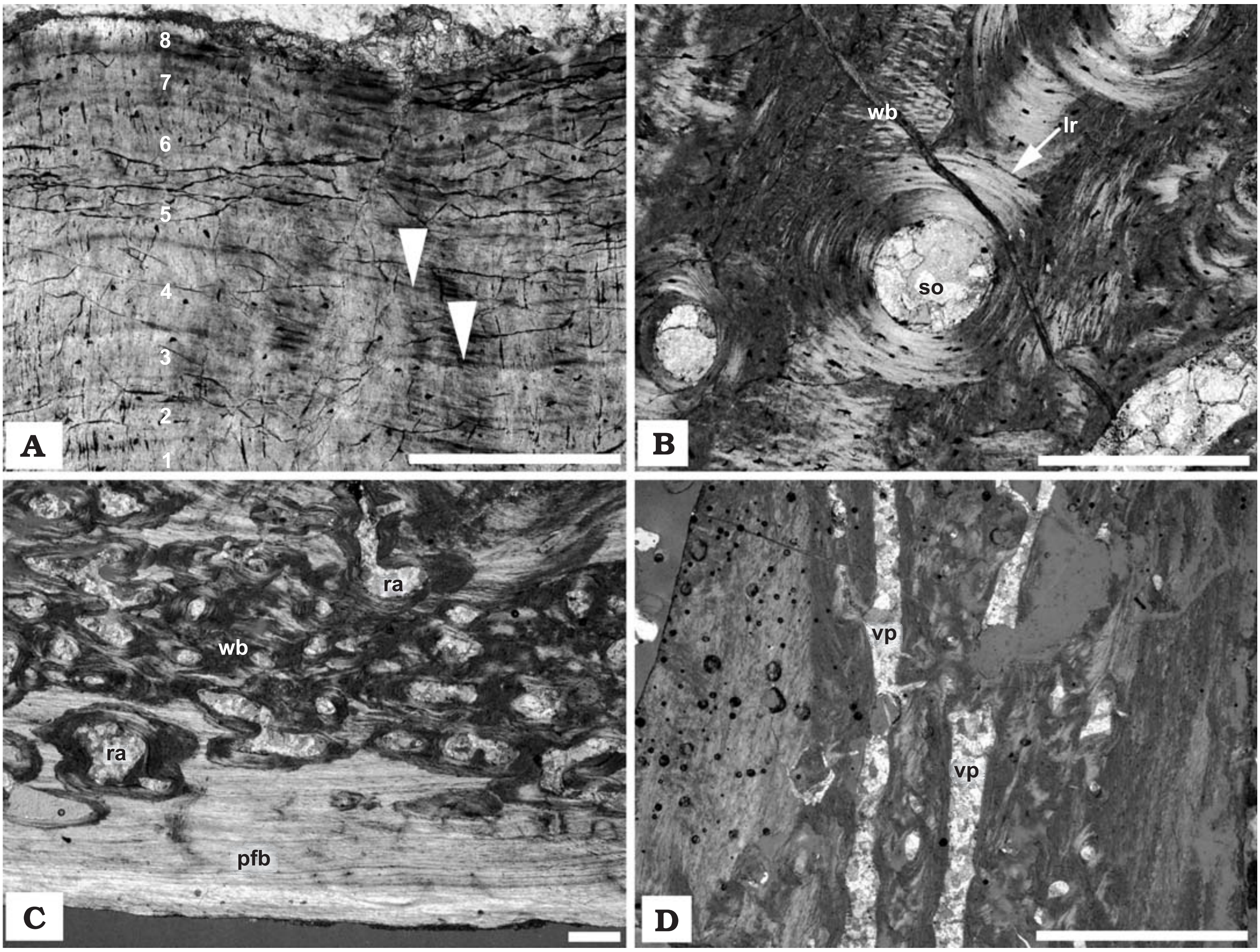

Fig. 3. *Akanthosuchus langstoni* O'Neill, Lucas, and Kues, 1981. Holotype, NMMNH P-8628, from the Middle Paleocene (Torrejonian) Nacimiento Formation, San Juan Basin, New Mexico, USA. Histological section of oval osteoderm. **A**. Superficial region of compact bone viewed under normal light, showing growth rings composed of multiple zones of lamellar bone (numbers) with intervening annuli, indicating the minimum age of the specimen at eight years. Note lines of arrested growth (arrowheads). **B**. Middle and deep regions of osteoderm viewed under cross-polarized light, showing primary woven bone, parallel-fibered bone, and elliptical resorption areas indicating obliquely oriented channels within the osteoderm. **C**. Detail of secondary osteon viewed under cross-polarized light, showing lines of reversal. **D**. Detail of vascular "pipes", channels that are elongated proximodistally within the spiked expansion of the osteoderm. Abbreviations: lr, line of reversal; pfb, parallel-fibered bone; ra, resorption area; so, secondary osteon; vp, vascular "pipes"; wb, woven bone. Scale bars 500 μm.

times longer than wide, in the case of the distalmost caudals). There is little or no development of regular, deep subcircular pitting. Instead, the ornamentation consists of shallow, irregular pits that merge with vascular traces. The keel of these osteoderms is relatively high, being at least one-half of the transverse dimension of the osteoderm base. The entire edge shows a pronounced, sharply crenulated texture.

The deep surfaces of dorsal osteoderms of *Alligator* are usually markedly smoother than their superficial surfaces. In the cases of nuchal, mid-dorsal, and dorsolateral osteoderms, as many as nine randomly arranged, tiny (~1 mm) neurovascular foramina pierce the deep surface. The deep surfaces of distal caudal osteoderms have an irregular texture, and are pierced by 3 to 5 small, centrally located foramina. Similar morphological variation was observed in isolated osteoderms of the extant crocodyline *Crocodylus rhombifer* (AMNH 77595), and indeed osteoderm morphology has been used extensively to differentiate between extant crocodylian species (e.g., Brazaitis 1973; Ross and Mayer 1983).

Histology.—Paleohistological sections of *Akanthosuchus* osteoderms (Fig. 3) reveal the presence of several distinct histological regions, as observed in many other crocodylomorphan taxa (Hill 2004; Scheyer and Sander 2004). The superficial surface of *Akanthosuchus* osteoderms is composed of compact, lamellar bone with eight observable zones separated by well-defined annuli. The compact bone in this region is avascular at its most superficial extent, but grades into more densely vascularized tissue, indicated by numerous obliquely oriented, ellipsoid channels.

Deep to the superficial compacta lies a region of trabecular bone that has undergone some remodeling by osteoclasts. This region contains a small amount of primary woven bone, upon which are superimposed numerous obliquely oriented resorption areas. Several secondary osteons are also present, intersecting with older structural units along lines of reversal. The deep layer of compact bone consists of mineralized fiber bundles oriented predominately parallel to the deep osteoderm surface. Under polarized light, this layer exhibits a uniform pattern of extinction.

Thin sections of one spiked osteoderm reveal the presence of large vascular channels running longitudinally within the distally expanded spike (Fig. 3D). This histological feature is similar to the vascular "pipes" observed in certain thyreophoran dinosaurs: (e.g., Buffrénil et al. 1986; Scheyer and Sander 2004; Main et al. 2005). Such "pipes" have been considered adaptations for thermoregulation in stegosaurs, potentially distributing a rich supply of blood around a bony scaffold, the osteoderm (Buffrénil et al. 1986). Main et al. (2005), however, concluded that the "pipes" were more likely related to the overall growth dynamics of specifically shaped osteoderms. Although many functions have been ascribed to osteoderms, we agree with Main et al. (2005), and suggest that the growth of a distally expanded spine accounts for the presence of elongated "pipes" in *Akanthosuchus* osteoderms. This interpretation may also explain the absence of such "pipes" from the oval osteoderm examined here, which is only gently keeled.

Phylogenetic analysis.—Re-examination of the holotype of *Akanthosuchus* allowed us to score six of Brochu's (1999) characters with certainty. The states of these characters in *Akanthosuchus* are described briefly below.

Character 18: All presacral vertebrae pertaining to *Akanthosuchus* possess procoelous centra (state 1), a condition found in all other eusuchians.

Character 35: With the exception of some flat, square osteoderms, nearly all osteoderms of *Akanthosuchus* bear a keel, spike, or blade (state 1).

Character 36: Some osteoderms of *Akanthosuchus* are perfectly square, while others are nearly as wide mediolaterally as they are craniocaudally long (i.e., approximately equant). *Akanthosuchus* lacks the wide, rectangular osteoderms that characterize certain basal alligatorines, diplocynodontines, and proximate crocodylian outgroups such as protosuchids (Colbert and Mook 1951; Erickson 1982; Norell and Clark 1990). We have scored *Akanthosuchus* as possessing equant or square osteoderms (state 1).

O'Neill et al. (1981) suggested two possible interpretations of the flat, square osteoderms associated with *Akanthosuchus*: they either represent an incomplete complement of ventral osteoderms or they represent armor that was confined to a specific region of the dorsolateral integument. Our observations support the former interpretation. The overall square shape and the presence of sutural boundaries on three of the four edges of these osteoderms indicate that they may have articulated laterally with adjacent ven-

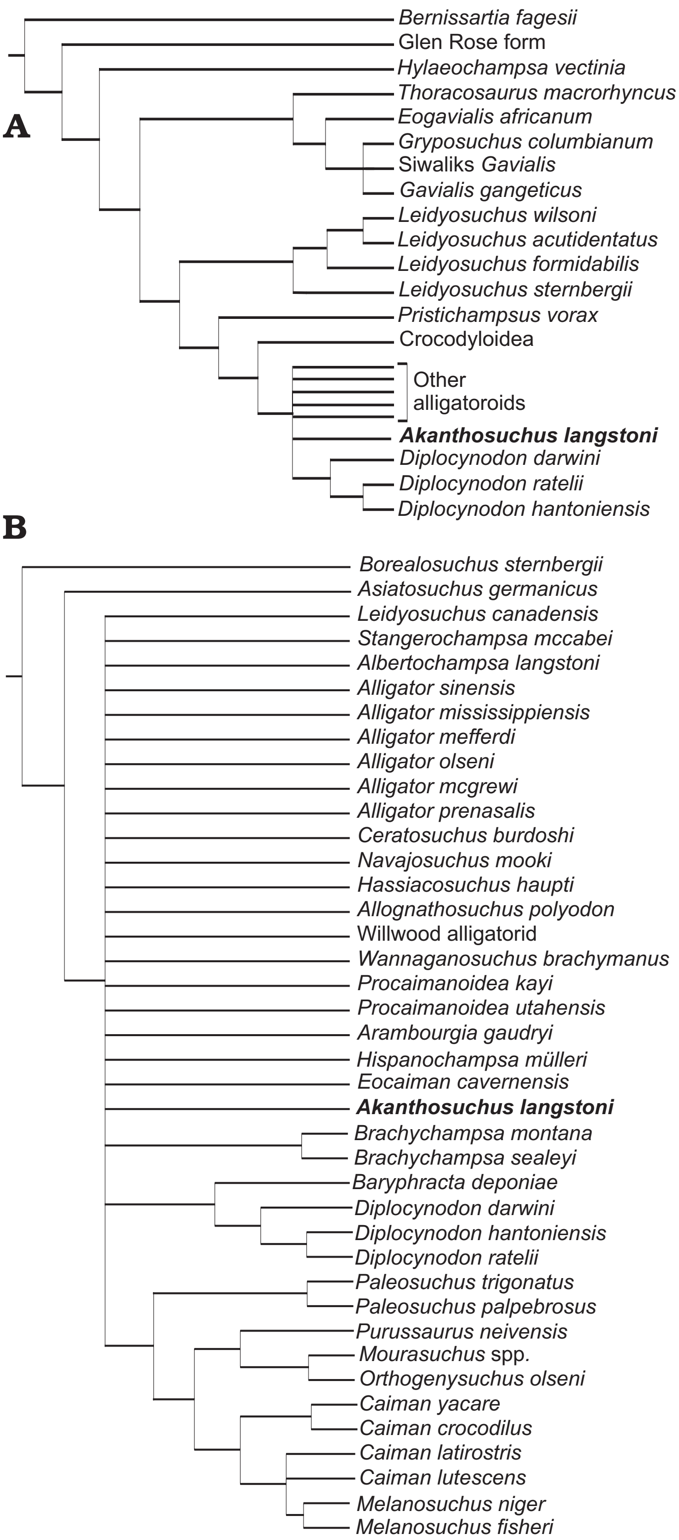

Fig. 4. Phylogenetic hypotheses indicating the relative position of *Akanthosuchus langstoni* among crocodylians. Trees are based on the results of heuristic searches using NONA (Goloboff 1994); see text for similar results obtained using PAUP (Swofford 2003). **A**. Strict consensus of 1446 trees using the matrix of Brochu (1999) with the addition of *Akanthosuchus* as a terminal taxon (TL = 468; CI = 43; RI = 83). **B**. Strict consensus of 82 equally most parsimonious trees using the matrix of Brochu (2004) with the addition of *Akanthosuchus* (TL = 253; CI = 58; RI = 80).

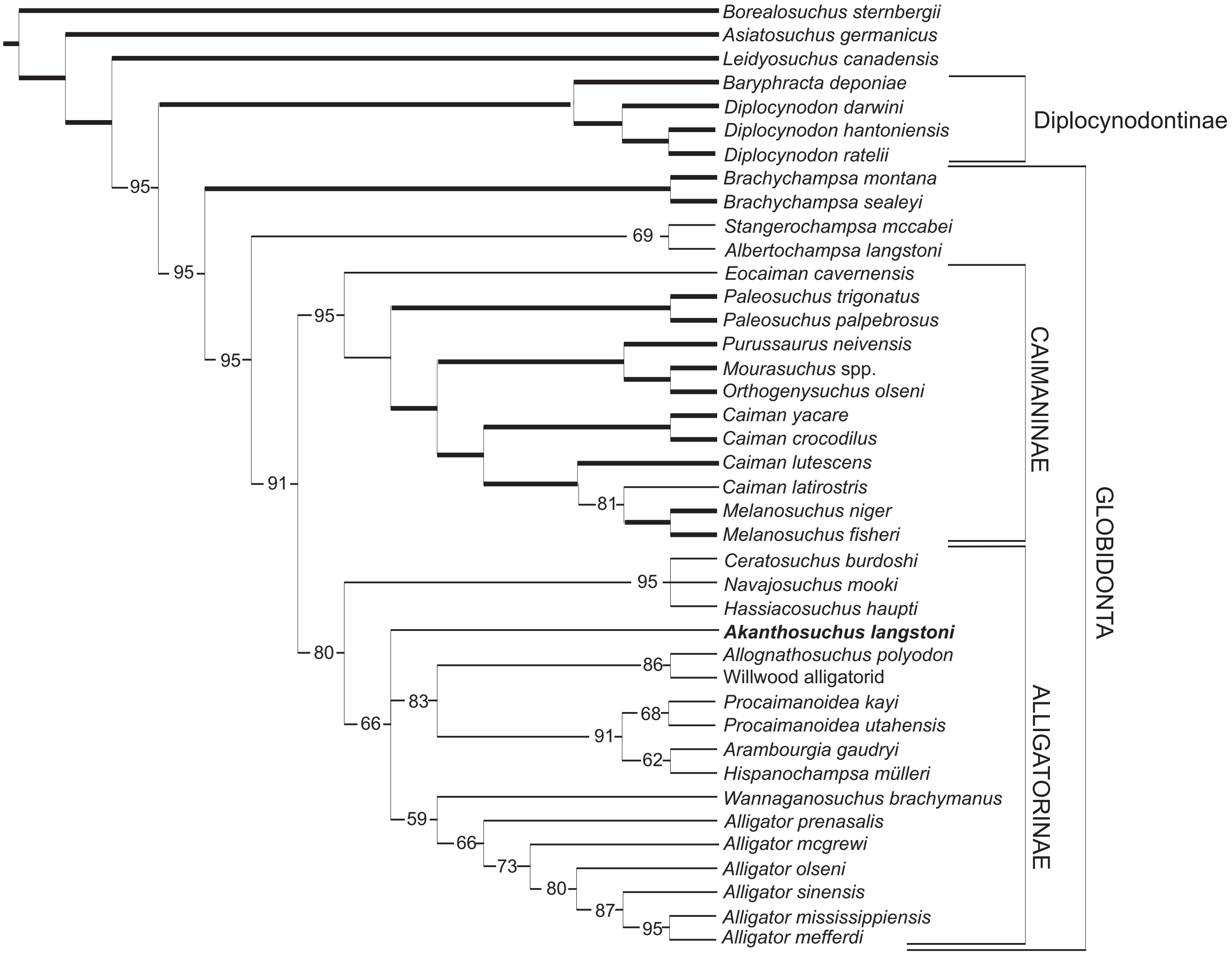

Fig. 5. Majority rule consensus of 82 equally most parsimonious trees obtained by analyzing the matrix of Brochu (2004) with the addition of *Akanthosuchus*. Bold lines indicate branches that are supported in 100% of trees (i.e., branches found in the strict consensus; Fig. 4B). Numbers indicate the percentage of trees that retain a particular branch when majority rule consensus is calculated using NONA; see text for similar results using PAUP.

tral osteoderms, and anteriorly with a small accessory osteoderm, as in modern caimans (CITES 1995; Brochu 1999). We have chosen to score Brochu's (1999) character 39 as ambiguous, however, because we cannot determine with certainty whether the square osteoderms actually represent ventral ossifications.

Character 40: The anterior margins of all *Akanthosuchus* osteoderms are smooth, and there is no development of an articular process (state 1).

Character 50: As in other eusuchians, the single known retroarticular process of *Akanthosuchus* is curved posterodorsally (state 1).

Character 51: The surangular does not extend to the posterior tip of the retroarticular process, but terminates well anterior to it (state 1).

Re-analysis of Brochu's (1999) data set using NONA yielded 36 equally most parsimonious trees, with a length of 479 steps each. The strict consensus of these trees is essentially congruent with the tree presented by Brochu (1999: figs. 22 and 23), with only a loss of resolution among members of Gavialoidea.

After adding *Akanthosuchus langstoni* to the matrix, an analysis under identical conditions in NONA resulted in 1446 equally most parsimonious trees, with a tree length of 468 steps. The strict consensus of these trees (Fig. 4A) is also largely congruent with Brochu's (1999) hypothesis based on morphology alone. It contains a monophyletic Alligatoroidea as the sister taxon to a monophyletic Crocodyloidea. Whereas the relationships among crocodyloids are well resolved, relationships among alligatoroids are almost completely unresolved. The three species of *Diplocynodon* are recovered as a monophyletic genus, but the remainder of Alligatoroidea is reduced to a polytomy that includes *Akanthosuchus langstoni*.

Based on these results, *Akanthosuchus* is unequivocally an alligatoroid, but its relationships to other alligatoroids remain unclear. To test the relationships of *A. langstoni* among other alligatoroids, we re-analyzed the matrix of Brochu (2004; a revised version of the matrix used by Brochu [1999] with three additional characters and only non-crocodyloid taxa included) with the inclusion of *Akanthosuchus*. Eighty-two most parsimonious trees were recovered, with a tree length of 253 steps. Calculating the strict consensus of these trees (Fig. 4B) again imparts a loss of resolution at certain deep nodes within the phylogeny, but several major clades are recovered as monophyletic. A monophyletic Diplocynodontinae (*sensu* Brochu 2004) is preserved in the strict consensus, as is a sister-taxon relationship between the two species of *Brachychampsa*. In addition, all caimanines more derived than *Eocaiman cavernosus* comprise a monophyletic clade that is fully congruent with the hypothesis of Brochu (2004). In this analysis, *Akanthosuchus* groups with a polychotomous assemblage that includes all alligatorines, *Albertochampsa langstoni*, *Stangerochampsa mccabei*, and *Eocaiman cavernosus*. Although it is clearly not nested among modern caimans, the question of whether *Akanthosuchus* is more closely allied with Caimaninae or Alligatorinae remains equivocal.

A majority rule consensus tree (Fig. 5) supports Brochu's (2004) hypothesis of a monophyletic Globidonta as the sister taxon to Diplocynodontinae, as well as a monophyletic Alligatoridae consisting of Alligatorinae and Caimaninae. Eighty percent of trees recover a monophyletic Alligatorinae that includes *Akanthosuchus*, a finding that weakly supports alligatorine affinities for the genus. None of the analyses performed here supports a sister-taxon relationship between *A. langstoni* and either *Ceratosuchus burdoshi* or *Navajosuchus mooki*. Instead, 95% of trees support a clade consisting of *C. burdoshi*, *N. mooki*, and *Hassiacosuchus haupti* as the sister taxon to all other alligatorines (including *A. langstoni*).

Comparable results were obtained using PAUP, although many more most parsimonious trees were recovered in each analysis. When *Akanthosuchus* was added to the matrix of Brochu (1999), PAUP recovered 481,540 most parsimonious trees. The strict consensus of these trees supports an alligatoroid position for *Akanthosuchus*, but reduces the remainder of Alligatoroidea to a polytomy with the exceptions of a monophyletic Diplocynodontinae and *Baryphracta*. Adding *Akanthosuchus* to the alligatoroid-only matrix of Brochu (2004) yielded 11,588 most parsimonious trees, the strict consensus of which was identical to that recovered in NONA (Fig. 4B). Results of the majority rule consensus were also similar to those obtained using NONA, with 75% of trees supporting alligatorine affinities for *Akanthosuchus*, and 98% supporting a *Hassiacosuchus*+*Navajosuchus*+*Ceratosuchus* clade.

An Adams consensus tree identified *Akanthoshuchus langstoni* as a "wildcard" taxon (Nixon and Wheeler 1992) that likely contributes to the loss of resolution within Alligatorinae. Nevertheless, the higher-level taxonomic relationships that emerge from this analysis clearly designate *A. langstoni* as an alligatoroid, and perhaps also an alligatorine.

Discussion

O'Neill et al. (1981) stated that although *Akanthosuchus langstoni* was unequivocally a crocodylian, the available material did not allow further taxonomic assessment. These authors suggested tentatively, however, that *A. langstoni* might have alligatoroid affinities, based on the presence of a gently convex medial surface of the retroarticular process. Incorporation of the species (but not the character) into current phylogenetic analyses corroborates this hypothesis, as *A. langstoni* is resolved as a member of a polytomy exclusive of a monophyletic Crocodyloidea.

The strict consensus also excludes *Akanthosuchus* from Diplocynodontinae and *Brachychampsa*. Because both of these taxa possess members with wide, rectangular osteoderms, at least one additional evolutionary step is incurred when moving *Akanthosuchus* into one of these clades *a posteriori*, making such hypotheses slightly less parsimonious. The loss of phylogenetic resolution apparently caused by the addition of highly incomplete fossil taxa has been recognized in this data set before, when the addition of *Leidyosuchus multidentatus* caused a sevenfold increase in the number of most parsimonious trees (Brochu 1997b). Majority rule consensus trees provide some support, albeit weak, that *Akanthosuchus* is closer to alligatorines than to caimanines.

Because no diagnostic cranial material is known for *Akanthosuchus*, O'Neill et al. (1981) entertained the possibility that the specimen might represent the postcranium of an already described genus. *Ceratosuchus* and *Navajosuchus*, Paleocene crocodylians for which skull material was already known, were suggested as plausible candidates. The current study does not support the hypothesis that *Akanthosuchus* is closely related to *Ceratosuchus* or *Navajosuchus*. Instead, *Ceratosuchus* is allied with *Navajosuchus mooki* and *Hassiacosuchus haupti*, two taxa that have been suggested to represent species of the genus *Allognathosuchus* (Berg 1966; Sullivan et al. 1988; Lucas and Estep 2000; but see Brochu 2004 for an opposing view).

The spiked osteoderms of *Akanthosuchus*, however unusual, are not unique among Crocodylia. Several other fossil species exhibit distally expanded keels or spikes, although none exhibits the combination of spiked osteoderms and tall, curved "bladed" osteoderms seen in *Akanthosuchus*. *Pinacosuchus mantiensis*, a putative crocodylian from the Upper Cretaceous of Utah, exhibits a variety of osteoderm morphologies, including rounded spikes, roof-like ridges, and flat, asymmetrical plates (Gilmore 1942). The subfossil (Holocene) crocodyline "*Crocodylus*" *robustus* (AMNH 3107) also possessed tall, keeled osteoderms; however, these differ from the osteoderms of *Akanthosuchus* in several regards. The highly keeled "*C.*" *robustus* osteoderms exhibit curved lateral margins and are symmetrical in dorsal view, whereas those of *Akanthosuchus* bear a straight, sutural edge and are asymmetrical. In addition, the keels or spikes of *Akanthosuchus* osteoderms are either centrally located or caudally displaced, whereas those of "*C.*" *robustus* dominate the entire craniocaudal length of the osteoderms. In this regard, the highly keeled "*C.*" *robustus* osteoderms are most similar to the distal caudal osteoderms observed in *Alligator* (Fig. 2D), while the spiked osteoderms of *Akanthosuchus* resemble more the paired nuchal elements of other extant and fossil crocodylians (see, e.g., Brazaitis 1973). The osteoderms of *Akanthosuchus* also differ substantially from those of *Allognathosuchus* and its putative synonyms, *Navajosuchus* and *Hassiacosuchus*, which are only slightly keeled and ornamented with a dense array of broad, circular to ovoid pits (e.g., AMNH 6780; Mook 1941; Lucas and Estep 2000; Brochu 2004).

The morphological data presented here allow some interpretation of the maturity of the type specimen of *Akanthosuchus*. Brochu (1996) found that crocodylian vertebrae exhibit closure of the neurocentral sutures in an ontogenetic sequence that proceeds from caudal to cranial. Whereas the most caudal neurocentral sutures are fused at hatching, the anterior cervical sutures do not fuse until full maturity. For this reason, the presence or absence of neurocentral fusion in the cervical vertebral series has been used as a test of maturity in fossil crocodylians (Brochu 1996).

All known vertebrae of the type specimen of *Akanthosuchus* possess fully fused neurocentral sutures. These vertebrae, however, represent posterior dorsal, sacral, and caudal vertebral regions only. Hence, Brochu's (1996) criterion cannot be used to assess the maturity of this specimen. An alternative means of assessing maturity involves skeletochronology, the interpretation of growth marks caused by the regular, seasonal growth of reptilian bone. Osteoderm skeletochronology has been shown to be a reliable predictor of age in the extant crocodylian *Crocodylus johnstoni* (Tucker 1997), and has been applied to questions of longevity in extinct crocodylians (e.g., Erickson and Brochu 1999). The annuli observed in the lamellar bone of *Akanthosuchus* osteoderms indicate that it was no younger than eight years old at the time of death. This fact, coupled with the relatively small size of the specimen, suggests that it may not have been fully mature at the time of death. Females of most extant crocodylian species require over nine years to reach sexual maturity, and males can require up to 20 years (e.g., Magnusson and Lima 1991; Magnusson and Sanaiotti 1995). These details notwithstanding, modern alligatoroids continue to increase in size well beyond the age of eight years and a confident assessment of growth trajectory cannot be made on the basis of a single specimen. Small size in crocodylians can be due to somatic immaturity, but may also be a consequence of lineage dwarfism, as in species of *Paleosuchus* and *Osteolaemus*.

A comprehensive study of comparative osteoderm histology in crocodylians is beyond the scope of this paper. Future analyses should incorporate morphological and histological data from osteoderms, because such data have been shown to affect phylogenetic hypotheses by increasing resolution in both basal and highly nested divisions within a given clade (Hill 2003, 2004, 2005). The vast majority of material pertaining to *Akanthosuchus* consists of osteoderms, indicating that comparative integumentary data will be especially pertinent if no additional cranial material of this species can be identified. Future collecting efforts concentrated in Puercan and Torrejonian beds of western North America, however, may yet yield additional material that can be referred to *Akanthosuchus*.

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